THE MAYA AND THE VEGETATION OF THE YUCATAN PENINSULA

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ABSTRACT.—Several hypotheses have been formulated to explain the composition and structure of the lowland tropical forest of the Yucatan Peninsula, in particular, the abundance and dominance of useful trees in mature forest communities. They commonly assume that forests in the lowland Maya area are man-made, but tend to dismiss or generalize environmental conditions in the area. Recent studies in northern Yucatan do not reflect the pattern described in the literature: abundance of useful trees in the forests. Why are useful trees, especially fruit-bearing trees, not present in all mature forest of the lowland Maya area? Our objectives are to (i) present a brief review of the literature concerning the origin of the vegetation in the Yucatan Peninsula; (ii) explain how the original vegetation structure could have changed under human influence, resulting in abundance of useful trees; and (iii) discuss the reason why useful trees are not present in all mature forest communities of the lowland Maya area, as generally assumed or suggested by many authors. The abundance of useful tree species in forests of the lowland Maya area was probably human-induced, through the years, without human assistance, they are now only present where the environmental conditions allow their survival. Even though the Maya may have played a significant role shaping the vegetation, rainfall is too variable to expect an even distribution of useful fruit-bearing trees without human assistance.

RESUMEN.—Se han formulado varias hipótesis para explicar la composición y estructura de los bosques tropicales de la Península de Yucatán, en particular, la abundancia y dominancia de especies arbóreas útiles en bosques maduros; y asumem que los bosques de las tierras bajas mayas son producto de la actividad humana, pero tienden a relegar o generalizar las condiciones medioambientales del área. Estudios recientes realizados en el norte de Yucatán no reflejan el patrón descrito en la literatura: abundancia de especies arbóreas útiles. Nuestros objetivos son: (i) presentar una breve revisión de la literatura referente al origen de la vegetación de las península; (ii) explicar como la estructura original de la vegetación pudo cambiar bajo la influencia humana y resultar en abundancia de especies arbóreas útilies; y (iii) discutir la razón por la que no están presentes estas especies en todas las comunidades boscosas de las tierras bajas mayas, tal como lo asumen o sugieren diversos autores. La abundancia de especies arbóreas útiles en los bosques de las tierras bajas mayas fue probablemente inducida por el hombre, al pasar los años, sin la asistencia humana, solo están presentes ahora donde las condiciones medioambientales se los permite. A pesar de que los mayas hayan jugado un papel significativo modificando las estructura de la vegetación, la

precipitacion es tan variable como para esperar una distribucion uniforme de especies arbóreas útiles sin asistencia humana.

RESUME.—On a formulé quelques divers hypothèses pour expliquer la composition et la structure de la forêt basse tropicalle de la Peninsule Yucatanne, particulairement l'abundance et dominance des arbres utiles dans les communautés forestales mûres. On suppose en générale que les forêts de la région basse des Maya soient de l'origine humaine, mais on congédie ou généralise les conditions environmentelles de la région. Les études recentes dans le Nord de la Yucatanne ne reflechissent pas les models décrit dans la literature: l'abundance des arbres utiles dans la forêt. Nos objectifs sont: (i) présenter un résumé bref de la literature concernante de l'origine de la végétation de la Peninsule Yucatanne; (ii) expliquer comme on pouvrait changer la structure originalle de la végétation sous l'influence humaine, avec le resultat de l'abundance des arbres utiles; et (iii) discouter pourquoi les arbres utiles ne se trouvent pas dans tous les communautes forestales mûres comme plusieurs auteurs ont supposé ou suggéré. L'abundance des espece des arbres utiles dans la forêt de la région basse du Maya est probablement de l'origine humaine. Après plusieurs années, sans l'influence humaine, les arbres se trouvent aujourd'hui seulement dans les sites où les conditions environmentelles permittent leur survivance. Bien que les Maya pouvront avoir joué un rôle important dans la formation de la végétation, la chute de pluie est trop variable pour s'attendre à une distribution unie des arbres fruitiers utiles sans l'aide humaine.

INTRODUCTION

Several hypotheses have been formulated to explain the composition and structure of the lowland tropical forests of the Yucatan Peninsula; in particular, the abundance of useful trees in mature forest communities (e.g., Barrera et al. 1977; Gomez-Pompa and Kaus 1987; Gomez-Pompa 1987; Gomez-Pompa et al. 1987; Rico-Gray et al. 1985, 1988b). These hypotheses assume that forests in the lowland Maya area are man-made and dominated by useful tree species, but tend to dismiss or generalize the environmental conditions in the area. Many studies on the interaction between man and vegetation were originally generated to explain the abundance of the ramon tree, Brosimum alicastrum Sw. (Moraceae), on or in the immediate surroundings of archaeological sites of the Maya, for example: (i) Folan et al. (1979) and Puleston (1972) proposed the abundance was clearly the result of human cultivation and management; (ii) Lambert and Arnason (1978, 1982) explained that archaeological sites are optimal environments for the ramon; (iii) Peters (1983) suggested that the atypical autoecological characteristics (phenology, breeding systems, productivity) of some ramon tree populations (Tikal) are the product of artificial selection practiced by the Maya; and (iv) Ogata (1990) suggests the abundance of ramon in the vicinity of archaeological sites reflects the defaunation activity of Post-Classic Maya. In summary, we group the explanations for the abundance and dominance of useful tree species in the Yucatecan forests into two main hypotheses (modified from Gomez-Pompa and Kaus 1987): (1) The abundance of useful tree species is a consequence of their biological characteristics, which enables them to be very successful during the natural regeneration process of the vegetation, or in occupying man-made ecological niches; and (2) The trees were present in the area before human occupancy but not necessarily abundant, and selection by man (protecting and cultivating) was the determinant factor to account for abundance.

Recent vegetation studies in northern Yucatan, near an archaeological site (Thien et al. 1982) and a Mayan village (Rico-Gray et al. 1988a, 1988b, and unpublished data), do not reflect the pattern described above: abundance of useful tree species. Why are useful trees, especially fruit-bearing trees, not present in all mature forests of the lowland Maya area? Our objectives are to: (i) present a brief review of the literature concerning the origin of the vegetation in the Yucatan Peninsula; (ii) explain how the original vegetation structure could have changed under human influence, resulting in the abundance of useful trees; and finally (iii) discuss the reason why useful trees are not present in all mature forest communities of the lowland Maya area, as generally assumed or suggested by many authors. The abundance of useful tree species in forests of the lowland Maya area was probably human-induced, through the years, without human assistance, they are now only present where the environmental conditions allow their survival. Even though the Maya may have played a significant role shaping the vegetation, rainfall is too variable to expect an even distribution of useful fruitbearing trees without human assistance.

BRIEF HISTORY OF THE VEGETATION OF THE YUCATAN PENINSULA

The vegetation of southeastern Mexico has experienced a series of changes as the result of abrupt temperature and precipitation fluctuations during the Pleistocene (Toledo 1982). The study of lake sediments (pollen) in the Peten area in Guatemala (Lewin 1984; Leyden 1984) and western Honduras (Rue 1987), suggest that the mesic tropical deciduous forest dominated by Brosimum originated during early Holocene, approximately 10,000 to 11,000 years ago. Forests to the north, the Mexican portion of the Yucatan Peninsula, would be considerably younger and more xericphytic. The abundance of Brosimum pollen, compared to pollen from other tree species characterizing this vegetation, probably is due to its relative abundance. Ramon is wind-pollinated (Peters 1983) and most of the other trees in the community are insect-pollinated, thus contributing few pollen grains to sediments (Rue 1987). With the appearance of savannas and open areas (milpas?), Brosimum dominance probably declined, as indicated by lower levels of its pollen in sediments, and the appearance of Melastomataceae, Byrsonima, and the presence of Maize/Zea (Rue 1987). This decrease in dominance is ascribed to the initial Maya occupation of the region (3,000-1,700 B.P. for the Peten in Guatemala, Leyden 1984; 3,000 B.P. for western Honduras, Rue 1987), and continuous use until the sixteenth century. At the same time, it is interesting to note the appearance and increase of pollen depositions of Cecropia and Trema (Leyden 1984; Rue 1987), two typical tropical deciduous forest pioneer tree genera, which probably reflects major vegetation recovery processes. Rue (1987) suggests that the lack of palynological evidence for any significant late Holocene climatic change in the present or previous Central American sequences, allows the assumption that all vegetational changes are human induced. A comparison between the list

of plant genera in the palynological analyses and the one presented by Miranda (1958) in his classical vegetation survey, reveals that tree species composition of the deciduous tropical forests of the lowland Maya area must have remained very similar since Maya occupation; the only significant changes must have occurred in the structure (diversity, abundance, dominance) of the vegetation.

CHANGES IN VEGETATION STRUCTURE AND DOMINANCE OF USEFUL TREES

Vegetation structure is subject to continuous change. Whether the change is due to the effect of natural forces or human activity, three main aspects should be considered when studying the recovery process of a denudated forest patch: the length of time the area was cleared, the type of activity during this period, and the extent of the clearing. Different combinations of these factors will yield forests with very similar or very different composition and structure, relative to the original. In order to start the regeneration process one factor common to any combination of the above is the need of a source of propagules, whether the seed bank already existing in the soil, the seed rain following abandonment, or regeneration from coppice trunks. Changes in vegetation structure were no doubt directly induced by the agrosilvicultural techniques of the Maya. On the other hand, the presence, relatively close to denudated forest areas, of mature, reproductive individuals of useful tree species, had undoubtedly a significant quantitative advantage over newcomers during forest regeneration that followed the abandonment of agricultural land or urban centers. Abundant seed rains from useful tree species could originate from trees directly managed in the forest (Bartlett 1935; Denevan et al. 1984; Soemarwoto & Soemarwoto 1982), from those growing in homegardens or in the pet kot, and from remnant forest tree individuals; seed movement from trees to open areas could have been effected by wind, bats (e.g., Peters 1983), other mammals, or birds (e.g., Scott & Martin 1984).

Present day Yucatecan Maya homegardens contain reproductive individuals of many useful tree species (Anderson 1952; Barrera 1980; Rico-Gray et al. 1988a, 1990; Vargas 1983). Ancient Maya followed this practice (Marcus 1982), thus the abundance of seeds from useful species is guaranteed after abandonment of a denudated forest area.

Gomez-Pompa et al. (1987) suggested that ancient Maya selected certain forest areas, the pet kot, to plant and protect useful tree species. These stone-walled, man-made forests are recognizable today in certain areas of Yucatan, and could also be an abundant source of seeds for useful trees.

In many instances, when a forest is cleared for agricultural purposes, a number of individual trees are left untouched for later use. It has been suggested that remnant trees will become natural perching sites for both migratory and resident birds (Guevara et al. 1986). Frugivorous birds will drop or regurgitate seeds and fruits which fall under the canopies, contributing to an accumulation of species, which make these remnant trees regeneration nuclei.

In summary, the useful trees of the Maya were present in the area prior to their arrival, and the changes in vegetation structure that followed this event were no doubt influenced directly or indirectly by their activities. This influence must have been particularly important in the number of seeds of useful species available for the colonization of abandoned agricultural land or urban centers.

FOREST COMPOSITION TODAY IN YUCATAN

If the presence of useful tree species was uniform in past Maya communities (Marcus 1982), as it is now (Rico-Gray et al. 1990), then: (1) Why are all forests in the Yucatan Peninsula not dominated by the same useful tree species (especially useful fruit-bearing trees)? (2) Why are certain Yucatecan forests, close to Maya archaeological sites or villages, not dominated by these useful trees? And (3) If a great variety of useful trees have been cultivated and protected in Maya homegardens for the past five centuries, why are they not present in forest communities today? In other words, why should widely used species as Brosimum alicastrum Sw. (Moraceae), Cedrela odorata L. (Meliaceae), Chrysophyllum cainito L. (Sapotaceae), Cordia dodecandra A.DC. (Boraginaceae), Crescentia cujete L. (Bignoniaceae), Ehretia tinifolia A.DC. (Boraginaceae), Enterolobium cyclocarpum (Jacq.) Griseb. (Leguminosae), Jacaratia mexicana A.DC. (Caricaceae), Manilkara achras (Miller) Fosberg (Sapotaceae), Melicoccus bijugatus Jacq. (Sapindaceae), Persea americana Miller (Lauraceae), Pouteria mammosa (L.) Cronquist (Sapotaceae), Psidium guajava L. (Myrtaceae), Swietenia macrophylla King (Meliaceae), be practically absent in northern Yucatean forests?

We think that the only way these questions can be answered is to consider the mosaic of ecological and environmental conditions prevalent in the peninsula; in short, the Yucatan Peninsula is not an ecological and environmental uniform unit. The answer given by locals of Tixcacaltuyub in central Yucatan, or Tixpeual in northern Yucatan, as to why these useful tree species are present in their village but not in the different-age forest communities that surround it, is that they are not there because they do not belong to that type of forest. To support this idea, we compared species composition (Sorensen Similarity Index) between the village homegardens and their surrounding forests (all shrubs and trees). The resulting similarities are, 18.2% for Tixcacaltuyub and 22.6% for Tixpeual. These low percent similarities can be explained by the presence of secondary species in the non-tended portions of the homegardens (mainly shrubs and a few non-important trees). The important homegarden trees and shrubs are only present in this environment surviving as tended species; they do not otherwise survive

Man-induced dominance of certain useful trees in forests of the Yucatan Peninsula has been reported; in general, areas with more than 1,100 mm of total annual precipitation. Bartlett (1935) reports abundance of Manilkara and Brosimum for forests in Belize and the Peten in Guatemala; and Rico-Gray et al. (1985) report a forest dominated by Manilkara, Brosimum, Bursera, Spondias, and Cedrela in the Yohaltun valley in Campeche. This forest characteristic does not seem to hold for forests in the dry portions of the peninsula, even though the surveys were conducted in the vicinity of an archaeological site (Thien et al. 1982) and a village (Rico-Gray et al. 1988a, 1988b). The latter forests have some useful tree species

(Chemas and Rico-Gray 1991), like *Gymnopodium floribundum* Rolfe (Polygonaceae), but lack the useful fruit-bearing trees (e.g., *B. alicastrum*, *C. cainito*, *M. achras*), and the important timber species (e.g., *C. odorata*, *E. cyclocarpus*, *S. macrophylla*). The only areas where individuals of these tree species may be found in the north and northwest portions of the Yucatan Peninsula are: the *cenotes*, with their special soil and humidity characteristics; the *pet kot*, a man-made forest (Gomez-Pompa *et al.* 1987); tended in villages, whether in homegardens or dispersed throughout the village (Smith and Cameron 1977; Rico-Gray *et al.* 1990); and in the *petenes*, a very particular coastal vegetation association (Rico-Gray 1982; Duran 1987; Rico-Gray *et al.* 1988c). Barrera (1982) argues that the presence of useful tree species (*Annona*, *Manilkara*, *Sabal*, *Swietenia*) in the *petenes* is the result of human activity.

CONCLUSION

It is clear from the analysis of the above information, that the presence today of useful tree species in mature forest communities of the Yucatan Peninsula is correlated with their ecological characteristics, whether or not they were introduced by the Maya in the past. In particular, their presence today in the drier portions of the peninsula has to be associated with present and not past human activity. Most of the useful tree species the Maya have been utilizing for at least the past six centuries are originally native to the southern, more humid, tropical forests of the peninsula (1,500 mm total annual rainfall), or were brought from similar humid forests of other areas (before and after the Spanish conquest, Marcus 1982). In the drier portions, these species cannot survive when an area is abandoned and are left to compete with native species in the recovery process of the vegetation. In short, even though useful species (especially fruit-bearing trees) must have been present in the whole peninsula associated with Mayan activity, the reason why they are not abundant, are not dominant, and, more dramatically, are not present in many Yucatecan forests (particularly those in northern Yucatan), is because they are not native to the flora and, consequently, cannot survive under the environmental conditions prevalent in the central to northwest portions of the Yucatan Peninsula. Tended species were brought from more humid areas of the peninsula, from other areas of Mexico, or from other countries; both before and after the Spanish conquest. The only places where we find combinations of these species in northern Yucatan Peninsula are the pet kot, the cenotes, the petenes, and tended in villages; it has been suggested that propagules of these species were brought by man to these areas.

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